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XXI.

CONTRIBUTIONS FROM THE ZOOLOGICAL LABORATORY OF
THE MUSEUM OF COMPARATIVE ZOOLOGY AT
HARVARD COLLEGE.XXIII.—PRELIMINARY NOTICE ON BUDDING IN
BRYOZOA.

BY C. B. DAVENPORT.

Presented February 11, 1891, by E. L. Mark.

SINCE several months must elapse before the publication of my studies on Budding in Bryozoa, it has been thought best to present, in a preliminary communication, some of the more important facts gained.

In my paper on *Cristatella*,* I described for that genus a mass of cells lying between the ectoderm and muscularis which gave rise, by active cell proliferation at certain regions, to the inner layer of the polypide,—the layer from which the inner lining of the kamptoderm, the outer layer of the tentacles, the nervous system, and the digestive epithelium arise. This inner layer has been brought into prominence by the conceptions of Hatschek concerning its significance,—conceptions which appear to have influenced some of his followers in their study of marine Bryozoa. According to Hatschek, this inner layer is to be regarded as entodermic in origin, and to give rise to the digestive epithelium only. The latter part of this view is certainly incorrect, as shown by the concurrent testimony of Braem and myself. It remained, however, to determine the *origin* of the layer, or rather of the stolonic mass from which it arises. The “stolonic mass” arises in the embryo, soon after the completion of the two-layered condition, from the ectoderm, at the same pole as that at which the so-called gastrulation takes place. A disk of cells sinks below the general level of the ectoderm and becomes overgrown by that layer. This disk expands rapidly at the base of the ectoderm, and in all directions of the plane, by cell proliferation, and gives rise to the first polypides. The first two

* *Cristatella: the Origin and Development of the Individual in the Colony.* Bull. of the Museum of Comp. Zoöl. at Harvard College, Vol. XX. No. 4, November, 1890.

polypides, one of which is slightly older than the other, arise so that their anal surfaces are turned towards each other.

The coelomic epithelium arises by a sort of ingestion, as observed by Korotneff, and is to be regarded, probably, as mesoderm plus entoderm, the entoderm being reduced to a still more rudimentary condition than in Gymnolæmata.

In *Plumatella*, the inner layer of the primary polypide arises near the pole of ingestion directly from the outer layer of the two-layered sac, and not from a mass which has already lost its connection with the outer layer, as in *Cristatella*. The second polypide arises at some distance from and wholly independently of the first, and, like it, by an invagination of the body-wall near the pole of ingestion. The remainder of the polypides are derived from the indifferent cells about and in the neck of these two primary ones.

The method of origin of the primary polypides is fundamentally the same in both genera, but the conditions in *Plumatella* are to be regarded as the more primitive. In both, the inner layer of the polypide is derived from the neutral region of the outer larval layer whence the inner larval layer has arisen. Possibly this region should be regarded as neither ectoderm nor entoderm, but as still indifferent, and capable of giving rise to either.

The origin of the primary bud in Gymnolæmata also is probably to be referred to the pole of ingestion or invagination, but owing to greater difficulties of orientation this cannot be determined so easily as in Phylactolæmata.

My studies on and drawings of *Paludicella* were already nearly completed when I first saw Braem's "Untersuchungen über die Bryozoen des süßen Wassers," in *Bibliotheca Zoologica*, Heft VI., 1891. With great keenness, he has been able, even by the study of the living animal, to correct some errors of previous authors, and he has anticipated some of my observations.

Each young polypide arises in the adult colony independently of any older polypide, from a mass of embryonic, rapidly dividing tissue at the tip of the branch, and some of this tissue is left behind as the tip moves forward. Typically, three masses of such tissue are left behind, at intervals corresponding to the joints of the branch. Of these three masses, one, the median, gives rise directly to the youngest polypide of the ancestral branch. The other two lie about 90° to the right and left of the median bud, and remain in a quiescent state until the median bud has attained a considerable size. The cells of these lateral masses are always distinguishable from those of the adjacent

body-wall by their cuboid form. They finally give rise to lateral branches, in which polypides are secondarily developed.

Braem has offered the ingenious hypothesis that the tip of the branch is to be regarded as having been occupied, ancestrally, by a polypide which has coenogenetically disappeared. Young polypides are on this assumption derived from the neck of older ones, as in Phylactolæmata. This hypothesis is rendered less necessary, if one conceives that in the budding process the younger bud is not derived from the older, but that *they are successively derived from the same mass of embryonic tissue*, — a view which I have already maintained concerning Phylactolæmata. *The tip of the branch is*, to my mind, *to be regarded as a stolon in both the median and lateral branches*. To form the polypide, the two layers of the embryonic mass of the wall are, in *Paludicella*, invaginated into the cœlom. But some of the cells remain in their indifferent condition as the neck of the polypide.

As Braem saw in the living animal, and as my sections and reconstructions sufficiently demonstrate, the hinder part of the alimentary tract arises in a manner comparable with that in Phylactolæmata, and its formation progresses from the anal towards the oral end. The œsophagus arises independently, and later the two pockets fuse to form the completed alimentary tract. The tentacles arise somewhat differently from those of Phylactolæmata, and in the manner recently described by Seeliger for *Bugula*, and they as well as the kamptoderm are here two-layered. They lie at first in two parallel rows of seven each. The anus is not removed outside the tentacular corona until the two posterior free ends of the ring canal meet and become confluent between mouth and anus. An odd tentacle, younger than the others, often arises directly oralwards of the anus. The brain arises as in *Cristatella*, and sends out two large circumœsophageal processes to form the commissure. The so-called *epistome* of Korotneff, Nitsche, and Seeliger, which they have believed to exist in the early stages of different Gymnolæmata, is merely the fold separating the brain cavity from the œsophagus, and has no relation to the epistome of Phylactolæmata or Endoprocta. I have found no trace of a true epistome at any stage. The body-wall is invaginated at the neck of the polypide, and the latter extends as a long cylinder for some distance below the general surface. It secretes the chitinous rods and cuticula of the adult "neck." The "collare setosum" appears to split off from the thick cuticula of the neck as a delicate chitinous cylinder, which has its distal end free and its proximal end embedded in the cells of the neck immediately around the atrial opening. From its

method of origin and structure, one finds it difficult to concur with the suggestion of Professor Ehlers, that the *collare setosum* of *Ctenostomata* is homologous with the cirri of *Endoprocta*. Muscles and funiculi both arise from the cells of the cœlomic epithelium. The communication plates arise as a circular fold of the body-wall. The cells of the cœlomic epithelium which immediately surround the central pole become metamorphosed at their inner ends to form the teeth of the central sieve.

The polypides of the *Bicellariidæ*, *Membraniporidæ*, and *Alcyoniidæ* arise in a similar manner to those of *Paludicella*; that is, from a mass of indifferent cells at the margin of the colony, — a mass from which the body-wall also is derived. The polypide arises in all cases by an invagination of the body-wall, which is two-layered at the margin of the colony. In all cases studied, the whole of the polypide is derived from this one rudiment. The alimentary tract arises, at least in some cases, exactly as in *Paludicella*. The ganglion arises from the inner layer of the bud, by an evagination of the floor of the atrium in both *Ctenostomata* and *Cheilostomata*, and I have found no trace of a genuine epistome at any stage.

Budding in marine *Gymnolæmata* seems to occur in accordance with certain laws, which may be deduced from a study of erect colonies like *Bugula*. In *Bugula turrita*, Verrill, we have a colony with an erect axis and branches whose points of insertion lie in a right or left handed spiral. The phyllotactic arrangement of the branches is not an invariable one, but is approximately $\frac{3}{8}$. Each branch is fan-shaped, the handle being the point of attachment, and is slightly concave toward the axis, like the thread of an Archimedean screw. The fans at the base of the colony are largest and oldest, at the tip youngest. The individuals are arranged end to end, in lines which spring from the single most proximal individual, and increase in number as upon this and the successively more distal individuals lateral as well as terminal buds arise. Sometimes, however, but one new bud — a terminal one — arises. The branches are not wholly separate from each other, but cling together in pairs.

The following laws of growth have been deduced: — 1. The individuals "break joints." 2. The lateral buds are formed earlier, and do not extend so far distally as the terminal buds. 3. When a terminal and lateral bud attached to the same proximal individual are each immediately followed by two buds, the two lateral buds lie adjacent, the two terminals outside. 4. Lateral buds tend to arise at the same time on two branches which spring from a common individual. 5. Law 4 is modified by a superior one, according to which lateral buds arise

more frequently at the edges of the fans than elsewhere. 6. The marginal branches are shortest, the middle ones longest. 7. There is one proximal individual to each "fan." This is followed by two, and these by four, of which four the two inner adjacent are lateral, the two outside ones terminal. Then each of the two outside individuals of these four bears more individuals, counting all which are formed between it and the periphery, than does each of the inner individuals. 8. New individuals are constantly being formed at the periphery of the fan, and at about the same time, but on some branches only one new bud arises, on others two. The tendency to give rise to two buds decreases as the fan grows older; and if a number of arcs be struck across an accurate drawing of an entire fan, with the proximal individual as a centre and with different radii, it will be found that the number of individuals cut by any linear unit of arc is the same for all radii.

In *Bugula flabellata* the fans are not attached to an erect axis, but are each attached to the rock or woodwork by their proximal individual. Three or five branches are united together, instead of two, as in *B. turrita*. The above "laws" are equally applicable to this species, except that No. 4 does not apply well here, being masked by another, namely, that of the three or five branches which are united together the outer ones only give rise to lateral buds. The above rules hold for *Crisia eburnea* also, which rises erect like *Bugula*, and has its branches united in pairs.

In genera which, like *Membranipora*, *Lepralia*, and *Escharella*, form creeping colonies in which all of the branches cling together, the normal architecture of the colony is obscured by inequalities of the surface upon which it lies. But under favorable conditions there is a tendency to conform to the laws which we discover in *Bugula*.

Regeneration of polypides has been studied in *Escharella* and *Flustra*. In these cases regeneration occurs at one point only; namely, on the operculum immediately behind, i. e. proximad of the atrial opening. Regenerated buds thus arise in the immediate vicinity of older ones, and from those cells some of which went to form that older polypide. They are formed by an invagination of the body-wall exactly as are the old polypides. Although the cells of the operculum have lost their cuboid form, and only return to it again in giving rise to the new bud, yet the nuclei appear to remain more abundant here than elsewhere on the body-wall, and this may perhaps be considered a condition of less extensive differentiation than obtains in all other parts of the body-wall.

CAMBRIDGE, February 9, 1891.